Biological Conservation 191 (2015) 67–74

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/bioc

Hotspots of predation persist outside marine reserves in the historically fished Mediterranean Sea

Jordi Boada [a,*], Rohan Arthur [b], Simone Farina [a,c], Yaiza Santana [a], Oriol Mascaró [a], Javier Romero [d], Teresa Alcoverro [a,b]

[a] Centre d'Estudis Avançats de Blanes (CEAB-CSIC), Accés a la cala Sant Francesc 14, 17300 Blanes, Spain
[b] Nature Conservation Foundation, 3076/5, 4th Cross, Gokulam Park, 570 002 Mysore, Karnataka, India
[c] Fondazione IMC, Centro Marino Internazionale Onlus, Localitá Sa Mardini, IT-09170 Torre Grande, Oristano, Italy
[d] Departament d'Ecologia, Facultad de Biologia, Universitat de Barcelona, Av. Diagonal, 643, 08028 Barcelona, Spain

ARTICLE INFO

Article history:
Received 27 March 2015
Received in revised form 7 June 2015
Accepted 13 June 2015
Available online xxxx

Keywords:
Predator–prey interactions
Refugia
Rhizome layer
Canopy height
Paracentrotus lividus
Macroalgal communities
Posidonia oceanica
Diplodus sargus

ABSTRACT

The Mediterranean Sea has sustained historically high levels of fishing since pre-Roman times. This once-abundant sea has witnessed major declines in apex predators, now largely restricted to isolated pockets within marine reserves. This depletion could critically impact macrophyte communities that are strongly structured by top-down processes. We evaluated rates of predation on the sea urchin *Paracentrotus lividus*, a key herbivore of macroalgal and *Posidonia oceanica* seagrass seascapes, across a large stretch of the Western Mediterranean coastline. Fish predation was generally higher inside reserves, but was equally high at several locations outside these boundaries. Although critically low at some locations compared to reserves, predation was functionally ubiquitous in most habitats, seasons and sites. Fish were still primarily responsible for this predation with no clear evidence of meso-predator release. Macroalgal habitats were consistently subject to higher predation than in seagrass meadows, functionally critical given the vulnerability of macroalgal systems to overgrazing. Predation hotspots were clearly associated with high fish predator numbers and low refuge availability. Taken together, these results suggest that long-term overfishing may not necessarily reflect a complete loss of trophic function. Pockets of fish predation may still persist, linked to habitat complexity, predator behavioral adaptations and landscape-level features. Given the essential role top-down control plays in macroalgal communities, regulating fishing at these predation hotspots is vital to effectively conserve habitats from future hysteretic shifts. Even historically fished seas may retain areas where trophic function persists; identifying these areas is critical to preserving the remaining ecological integrity of these coastlines.

1. Introduction

One of the clearest signatures of the increasing human imprint on the biosphere is the gradual weakening of trophic processes as top predators decline from natural ecosystems under the combined onslaught of direct extraction and habitat loss (Ripple et al., 2014). Predation is a critical agent of community structuring (Hairston, Smith, & Slobodkin, 1960); the depletion of key predators leaves both terrestrial and marine ecosystems increasingly prone to catastrophic and often hysteretic collapses from which recovery can be protracted. Marine macrophyte communities are particularly susceptible; uncontrolled by predation, marine herbivores can undergo major population explosions, overgrazing macrophyte-dominated ecosystems (Kempf, 1962). In a classic example, otters have been identified as principal structuring agents of kelp communities in the Eastern Pacific by regulating urchin populations (Tegner & Dayton, 2000). Similarly, the structuring of Western Mediterranean macrophytes appears to be strongly mediated by top-down control of urchins by fish predators (Pinnegar et al., 2000).

Marine ecosystem managers have long recognized the importance of conserving higher trophic functions, and regulating fishing of top predators has been the instrument of choice in managing nearshore ecosystems (Estes et al., 2011). There has been a growing call to expand networks of marine reserves and impose fishing restrictions to protect key predators and enhance the natural resilience of the ecosystems they structure (Pinnegar et al., 2000). This is predicated on the assumption that fish predator numbers link well with rates of predation, and that healthy predator populations will ensure their functional roles within the ecosystem (Clemente, Hernandez, Rodríguez, & Brito, 2010). There is growing evidence demonstrating that marine reserves have been largely effective in reversing the direct and indirect effects of trophic decline (Shears & Babcock, 2002), and they clearly enhance ecosystem functioning. However, it is becoming increasingly clear that predation is an inherently dynamic process, and predator–prey

* Corresponding author.
E-mail addresses: jboada@ceab.csic.es (J. Boada), rohan@ncf-india.org (R. Arthur), s.farina@imc-it.org (S. Farina), yaizasbq@gmail.es (Y. Santana), omascaro@ceab.csic.es (O. Mascaró), jromero@ub.edu (J. Romero), teresa@ceab.csic.es (T. Alcoverro).

http://dx.doi.org/10.1016/j.biocon.2015.06.017

interactions can vary considerably across the seascape. The distribution and densities of predators and prey within the mosaic may be influenced by recruit supply, which may, in turn, be mediated by habitat differences (Hereu, Zabala, Linares, & Sala, 2004). Independent of numbers, predator–prey interactions may be strongly driven by how both predators and their prey use these habitats (Farina et al., 2014). These habitat-specific factors may also interact in complex ways making predator–prey interactions often difficult to predict. Both fish predators and their prey may modify their behaviors in relation to each other's presence, the abundance of conspecifics, the availability of refugia and the configuration of the habitat within the larger seascape. For instance, habitat structural complexity, by modifying the presence of prey refugia is fundamental in determining predation rates and, in turn, prey population structures (Farina, Tomas, Prado, Romero, & Alcoverro, 2009; Hereu, Zabala, Linares, & Sala, 2005). Moreover, predators may also be implicated in complex indirect interactions in macrophyte communities; fish herbivores, by reducing the leaf canopy of macrophyte communities, can enhance fish predation on urchin herbivores by reducing refuge availability (Pagès et al., 2012). Further, a reduction of top predators can sometimes lead to the competitive release of benthic meso-predators that may potentially compensate rates of functional predation experienced by the system (Levi & Wilmers, 2012). This can also be highly habitat dependent since every system could be host to a very different suite of predators. Finally, both predators and prey may move between habitats in the mosaic, and predation may be strongly influenced by patterns of habitat connectivity or isolation within the larger seascape (Hitt, Pittman, & Nemeth, 2011).

Two macrophyte habitats dominate the North Western Mediterranean: *Posidonia oceanica* seagrass meadows and shallow macroalgae-dominated rocky habitats, both potentially structured by top-down control of the herbivorous sea urchin *Paracentrotus lividus* (Fig. 1) (Verlaque, 1987). The Mediterranean has been seriously overfished for millennia (Sala et al., 2012), and determining if predation still plays a functional role is essential to planning conservation actions across the region (e.g. creations of marine reserves, management of coastal

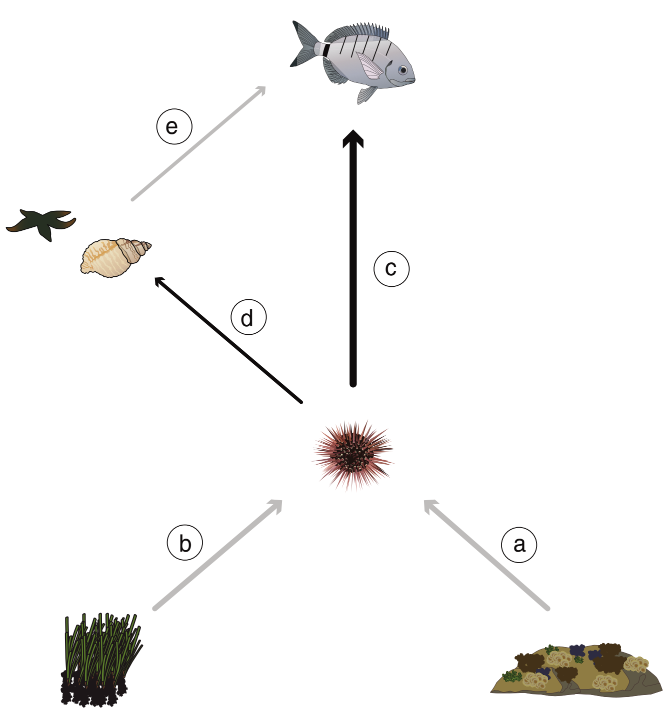

Fig. 1. Principal interactions in Mediterranean macrophyte communities. The sea urchin *Paracentrotus lividus* lives in both seagrass meadows of *Posidonia oceanica* and macroalgal dominated rocky habitats in the Mediterranean. Letters represent trophic interactions; herbivory (a) and (b), and predation (c), (d) and (e). Black arrows show the predator–prey interactions studied in the present work.

development). While it is well established that predation intensity is relatively high inside existing protected areas (Sala & Zabala, 1996) it is unclear to what extent this function is conserved beyond their boundaries, although it is generally assumed to be low because of this historically sustained fishing pressure (Guidetti et al., 2010). However, there is little information available on the factors that influence predation in different macrophyte habitats. The decline of fish predators could have triggered a functional substitution by other benthic predators. In addition, given that reserves are principally established to enhance predator numbers, understanding how predation activity is linked to fish predator abundance is critical. To answer these questions, we measured relative rates of sea urchin predation by fish and benthic predators at eight representative locations across a large stretch of the NW Mediterranean coast in both algal communities and seagrass meadows in different seasons. In addition, we attempted to identify if predator habitat use or habitat-specific factors (presence of refuges) can drive functional rates of predation in these dominant macrophyte habitats.

2. Materials and methods

2.1. Study system

The shallow seascape of the Western Mediterranean is dominated by rocky macroalgal communities and *P. oceanica* seagrass meadows. Although the sea urchin *P. lividus* is a key herbivore in both habitats, they may differ considerably in their susceptibility to urchin herbivory (Boudouresque & Verlaque, 2001). In macroalgal systems, urchin overgrazing can cause ecosystem barrens from which recovery is often protracted (Pinnegar et al., 2000). Predators likely play a vital role in regulating sea urchin populations (Supplementary, A1), preventing these ecosystem shifts (Guidetti, 2004; Sala, 1997). While *P. oceanica* meadows may experience very similar rates of urchin herbivory, they may cope better with this offtake because of their inherent evolutionary adaptations (Vergés, Pérez, Alcoverro, & Romero, 2008). However, heavy eutrophication could make meadows susceptible to overgrazing (Ruiz, Pérez, Romero, & Tomas, 2009). Several fish species prey on *P. lividus*, and many of these are important commercial and recreational fishery targets (Guidetti, 2006). Additionally, benthic predators including starfish and some gastropods may also be important contributors to sea urchin predation (Boudouresque & Verlaque, 2001).

2.2. Study site and sampling design

The study was conducted along the NW Mediterranean (~600 km). Eight sites were selected along the coast, characterized by shallow seagrass *P. oceanica* habitats and photophilic macroalgae on rocky substrates (Fig. 2). Sites were not randomly selected since all sites required both habitats to be present and at least one unfished reserve was required for the study objectives. Fishing is permitted at all sites except the Medes Island Marine Protected Area, which has been a marine reserve since 1990, and partially controlled in Portlligat since 2006 as part of the Cap de Creus Natural Park but with low fishing regulation. The reserve is characterized by high abundance and biomass of predatory fish (Garcia-Rubies, Hereu, & Zabala, 2013). In each habitat we assessed predation on the sea urchin *P. lividus*, the most important key herbivore in NW Mediterranean macrophyte habitats (Harmelin, Bouchon, Duval, & Hong, 1980). We evaluated predation impact by fish and benthic predators (see below) in each of the selected sites in summer and winter. In addition, we estimated the habitat use by the most important urchin predators, and evaluated habitat characteristics that could constitute an effective predation refuge for the urchin (i.e. canopy height in both habitats, crevices in rocky substrates and bare root-rhizome layer in seagrass meadows) (Orth, Kenneth, Heck, & van Montfrans, 1984). All measurements were recorded within a depth range of 3 to 8 m for both habitats.